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Fine-scale to flora-wide phylogenetic perspectives on Californian plant diversity, endemism, and conservation

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The California Floristic Province (CA-FP) encompasses North America's Mediterranean-type climatic region and is a global biodiversity hotspot in temperate North America. Fine-scale phylogenetic studies and increasing scrutiny of morphological, ecological, and geographic variation in the CA-FP vascular flora continue to reveal novel, often cryptic diversity warranting taxonomic attention. The prevalence of such discoveries warrants caution about potential for loss of undescribed or unrecognized biodiversity from human-related impacts, including insufficiently informed conservation-related actions (e.g., genetic augmentation or assisted migration). Broader-scale molecular phylogenetic studies have yielded other examples of more extensive CA-FP diversification than previously resolved.

For example, clades uniting CA-FP taxa not earlier thought to be such close relatives have been discovered in a wide diversity of tribes of composites and legumes. This understanding adds additional weight to the conclusions of Raven and Axelrod that in situ evolution, especially since the pronounced mid-Miocene transition toward summer-drying, has been a major factor in the origins of Californian vascular plant diversity. The importance of paleo-endemism in gymnosperms and (especially woody) angiosperms of the CA-FP flora also has been corroborated and refined by molecular phylogenetic studies, with improved understanding of the timing of divergence and relationships of isolated lineages, such as the extinct island-endemic *Hesperelaea* (Oleaceae). On a regional scale, studies of spatial patterns of Californian species richness, phylogenetic diversity, and phylogenetic endemism by the California Plant Phylodiversity Project (CPPP) have reinforced the floristic importance of areas of high topographic complexity, or environmental heterogeneity more generally, where relatively high levels of habitat diversity, speciation, and lineage persistence may be expected. The CPPP's finding that particularly young plant lineages and significantly high phylogenetic endemism are concentrated in drier regions of the CA-FP and in the adjacent Californian deserts has corroborated earlier preliminary findings and aligns with Stebbins's hypothesis of aridity as an evolutionary stimulus. A recent conservation gap analysis by the CPPP incorporating flora-wide phylogenetic and geographic occurrence data plus land-protection status and habitat-integrity information for California has demonstrated the potential of an integrative, evolutionary approach for identifying high-priority land conservation targets.

The California Floristic Province (CA-FP; Howell 1957; Raven & Axelrod 1978) is a global-scale biodiversity hotspot, one of only two recognized by Conservation International that occur largely or entirely within North America north of Mexico (Mittermeier et al., 2011; Noss et al., 2015), with ~42% of ~6900 minimum-rank taxa (i.e., species plus non-redundant subspecies and varieties) of native vascular plants endemic to the region (Burge et al., 2016). Such high endemism and concentrated taxonomic richness are common features of the five Mediterranean-type climatic areas worldwide (Cowling et al., 1996; Rundel et al., 2016). Late Cenozoic climatic change coupled with geological dynamism on a vast scale, and resulting topographic, edaphic, and climatic heterogeneity across the region, have been implicated in extensive diversification of the California flora, with an abundance of neo-endemic lineages and high beta-diversity (see Raven & Axelrod, 1978; Harrison, 2013; Anacker & Strauss, 2014; Baldwin, 2014; Schierenbeck, 2014). Development after mid-Miocene (~15 Ma) of the summer drought characteristic of the CA-FP today likely resulted in major ecological

opportunities for plant taxa preadapted to such conditions, following extinction of a wide diversity of taxa today associated with wetter summer conditions in eastern North America, the neo-tropics, and Asia (Raven & Axelrod, 1978; Axelrod & Schorn, 1994; Jacobs et al., 2004). In addition, persistence of pockets of relatively equable climate through time, such as in the Channel Islands and Klamath Ranges (Raven & Axelrod, 1978), and the potential buffering effects of topographic heterogeneity on climate change — by allowing for only short-distance migration to track geographic shifts in plant climatic niche space (Lancaster & Kay, 2013) — also have been considered important explanations for high floristic richness and endemism in California, by limiting extinction.

The foundational, synthetic study of patterns of diversity in California's flora by Raven & Axelrod (1978), building on the work of Stebbins & Major (1965), was informed in part by insights from the great wealth of experimental biosystematic investigations focused on Californian plants in the preceding decades. Over the past 30 years, molecular phylogenetic investigations have been increasingly applied to diverse questions in Californian floristics and have resulted in significant progress in extending the findings of Raven & Axelrod (1978) and earlier researchers. Here, I highlight select examples from three different scales of molecular phylogenetic inquiry that have yielded refined perspectives on California's floristic diversity and its conservation.

Fine-scale lineage diversity revealed by molecular phylogenetic studies. In the early 1990s, when DNA sequencing for plant systematic studies began in earnest, California floristics was already being reinvigorated by exciting field discoveries by sharp-eyed botanists working in promising, under-collected areas and by revision of floristic treatments for California's vascular plants in *The Jepson Manual* (Hickman, 1993). Ertter (2000) noted that a predicted decline in the rate of description of new endemic plant taxa in California following publication of *The Jepson Manual* had not occurred and that new taxa were being described at a rate that had not abated over the past century. Since then, the efforts of well-focused field botanists toward advancing California floristics have continued to bear fruit. For example, the earlier discovery of a new Californian paleo-endemic, *Neviusia cliftonii* Shevock, Ertter & D.W. Taylor (Rosaceae), in the limestone/metasedimentary country of the Shasta Lake region in 1992, has been followed in the past six years alone with descriptions of a wide diversity of new vascular plants from the same general area, e.g., *Adiantum shastense* Huiet & A.R. Sm. (Pteridaceae), *Erythranthe taylorii* G.L. Nesom (Phrymaceae), *Erythronium shastense* D.A. York, J.K. Nelson & D.W. Taylor (Liliaceae), and *Vaccinium shastense* J.K. Nelson & Lindstrand subsp. *shastense* (Ericaceae).

As molecular phylogenetic studies have come closer to achieving understanding of the main clades constituting the vascular plant tree-of-life (see Stevens, 2017), increasing effort has been focused on more detailed phylogenetic questions that bear on taxonomy at the finest levels. Earlier indications that discoveries of Californian plant lineages worthy of taxonomic recognition would accelerate by sampling across the morphological, geographic, and ecological ranges of accepted species in molecular phylogenetic studies (see Baldwin, 2000) have become realized over the past two decades, even in genera or higher-level taxa that were subjects of previous experimental biosystematic study, such as *Claytonia* (Montiaceae), *Collinsia* (Plantaginaceae), Madiinae (Compositae), Polemoniaceae, and Phrymaceae (see below).

Much of the progress in discovering fine-scale evolutionary lineages has been achieved in clades that have been long appreciated as diverse and taxonomically difficult. In *Claytonia*, for example, Stoughton et al. (2017, 2018) resolved extensive clade diversity within the *C. lanceolata* Pursh complex, with recognition of three morphologically and ecologically distinctive species in addition to *C. lanceolata* sensu stricto for the montane CA-FP, including *C. obovata* Rydb. and *C. serpenticola* Stoughton from different edaphic settings in the North Coast and Klamath ranges and *C. peirsonii* (Munz & I.M. Johnst.) Stoughton from the Transverse Ranges, plus a new species for the Mojave Desert, *C. panamintensis* Stoughton. In *Navarretia* (Polemoniaceae), Johnson et al. (2013) recognized four, morphologically and ecologically distinguishable species in California that had previously been treated within *N. intertexta* (Benth.) Hook., including two new-to-science sister species endemic to serpentine soils on opposite sides of the Great Central Valley, *N. paradoxiclara* L.A. Johnson & D. Gowen (Sierra Nevada) and *N. paradoxinota* L.A. Johnson & D. Gowen (Inner North Coast Ranges). Serpentine endemics, noted to account for ~12.5% of endemic taxa in California (Safford et al., 2005), and other edaphically restricted lineages are well represented among recent discoveries from phylogenetic analyses. The two most diverse genera of monkeyflowers, *Diplacus* and *Erythranthe* (Phrymaceae), are prominent examples of intensively studied clades that include recently recognized edaphic endemics among the ~23 newly described or reinstated monkeyflower species for California treated in the latest *Jepson eFlora* revision (Fraga, 2018).

Newly discovered evolutionary lineages in the California flora often appear to be eco-geographically distinct from close relatives, sometimes on a fine spatial scale in environmentally heterogeneous areas, as resolved in *Collinsia*

(Plantaginaceae) for the *C.* "metamorphica" complex (Baldwin et al., 2011). The complex — a current subject of taxonomic attention (M.S. Park, B.G. Baldwin, W.S. Armbruster, in prep.) — is an evolutionarily isolated clade within *Collinsia* that is endemic to metamorphics of the upper Merced River drainage in the central Sierra Nevada and previously misassigned to *C. linearis* A. Gray, a Klamath Ranges endemic. Within the "metamorphica" complex, three lineages that differ in corolla color and shape (Fig. 1a–c) occur in different environmental settings in distinct parts of the upper Merced River watershed, where a diversity of other narrow endemics occur, including Lewis's (1962) famous example of speciation by catastrophic selection, *Clarkia lingulata* F.H. Lewis & M.E. Lewis. Such findings warrant continued exploration for undescribed plant lineages within Californian areas known to harbor concentrations of endemics.

The degree to which Californian plant lineages recently discovered with the aid of molecular phylogenetic data represent cryptic diversity often requires consideration of whether distinctive morphological characteristics are evident in live material as opposed to herbarium collections. Pressing and drying of specimens may render floral characteristics inconspicuous that are distinctive and easily observed in live plants, as in some of the examples discussed above, or may fail to capture diagnostic characteristics that are not evident when plants are usually collected, such as basal leaf lobing in herbs that flower after rosettes generally have withered, as in the *Layia gaillardioides* (Hook. & Arn.) DC. complex (Baldwin, 2000, 2006, in prep.). Characterization of such newly discovered diversity as cryptic may serve to emphasize the taxonomic value of molecular phylogenetic data but potentially at the expense of communicating that those discoveries represent phenotypically distinct lineages that are practical and important to recognize and conserve.

Recent discoveries of fine-scale Californian plant diversity warranting taxonomic recognition also serve to demonstrate how phenotypic change accompanying diversification may be driven by ecological factors not necessarily reflected strongly by morphology. For example, resolution of multiple host-specific evolutionary lineages within long recognized holoparasitic taxa of New World broomrapes in *Aphyllon* sect. *Aphyllon* (= *Orobanche* sect. *Gymnocaulis*; Orobanchaceae) is consistent with the hypothesis that host shifts often have driven diversification with relatively minor accompanying morphological change (Schneider et al., 2016). Among those lineages, a sister pair nearly endemic to the CA-FP and now treated as *A. epigalium* Colwell & A.C. Schneid. subsp. *epigalium* and *A. epigalium* subsp. *notocalifornicum* Colwell & A.C. Schneid. (Colwell et al., 2017) is specific to hosts in *Galium* (Rubiaceae) and provides the first detected

example in *Aphyllon* of horizontal gene transfer from host to parasite (Schneider et al., 2018). *Aphyllon epigalium* also exemplifies the potential value for biodiversity discovery of old herbarium specimens and accompanying archives: W. L. Jepson noted in his 1918 fieldbook entry for collection no. 6385 that specimens now referable to *A. epigalium* were somewhat unusual morphologically, with characteristics that help to diagnose the recently described species (Colwell et al., 2017).

Continuing phylogenetic efforts on California tarweeds (subtribe Madiinae; Compositae) and in related Californian genera in other subtribes of tribe Madieae have resolved additional, rare evolutionary lineages worthy of formal recognition in widespread taxa, such as *Calycadenia pauciflora* A. Gray (Baldwin, 2003, in prep.) and *Layia gaillardioides* (Baldwin, 2006, in prep.), as well as in rare and endangered taxa, such as *Blepharizonia plumosa* (Kellogg) Greene, *Carlquistia muirii* (A. Gray) B.G. Baldwin, and *Centromadia parryi* (Greene) Greene subsp. *congdonii* (B.L. Rob. & Greenm.) B.G. Baldwin (B.G. Baldwin, in prep.). Taxonomic recognition of undescribed tarweed lineages is a priority not only for their conservation but also for conservation of any organisms that are ecologically dependent on tarweeds. Some lineages of flower moths in *Heliothodes* and *Microhelia* (Heliothinae), for example, are obligate tarweed associates, with larvae that feed on tarweed foliage (Krimmel & Pearse, 2013) and show various degrees of specialization to particular tarweed clades (T. A. Sears, pers. comm.). The potential importance of rare plants to survival of other rare organisms, such as endemic insects, is sobering in light of the sizable frontier in arthropod systematics that remains to be explored in California (Powell & Hogue, 1979) and evidence for elaborate food webs associated with some native plants, such as tarweeds (LoPresti et al., 2018).

The above examples of newly discovered evolutionary lineages of Californian plants were selected from a large diversity of similar findings that serve to reinforce the need for investment in more detailed systematic and taxonomic studies of the California flora and associated biota. The urgency of that task is growing rapidly with accelerating anthropogenic impacts to Californian ecosystems (e.g., Rapacciuolo et al., 2014; Chornesky et al., 2015) and the need for finer-scale systematic data to inform efforts aimed at conserving biodiversity in the face of habitat fragmentation and climate change. For example, scientific discussion about restoration-focused conservation actions, such as genetic augmentation of plant populations and assisted migration, has been principally focused around important ecological and population-genetic considerations (e.g., Broadhurst et al., 2008; Weeks et al., 2011; Ottewell et al., 2016), but generally

does not extend to the possibility that current taxonomy may fail to reflect evolutionary diversity warranting recognition and protection. As a result, there is potential for loss of irreplaceable but unrecognized biodiversity by genetic swamping or ecological displacement of undescribed evolutionary lineages by intentionally introduced relatives (see Levin et al., 1996; Soltis & Gitzendanner, 1999; Baldwin, 2000; Balao et al., 2015; Gómez et al., 2015; Todesco et al., 2016). Once such irreversible actions are implemented, it may no longer be possible to even discern what was lost, and such hidden extirpations or extinctions could take with them the ability to understand much about the evolutionary and ecological history of the California flora, as the wild genetic and evolutionary structure of plant lineages is forever altered.

Broader-scale phylogenetic perspectives on magnitude and timing of Californian diversification. Advances in understanding of deeper-level relationships and lineage ages from phylogenetic investigations have reinforced and extended the conclusions of Raven and Axelrod (1978) that the bulk of endemic plant diversity in the CA-FP stems from diversification since mid-Miocene in clades centered in North America, especially western North America (see Baldwin, 2014). Phylogenetic findings have warranted a rethinking of the geography of speciation and the evolution of disparity in some diverse or complex families or genera, sometimes necessitating a revision of generic or higher-level taxonomy. For example, in each of the two most species-rich Californian plant families — Compositae and Leguminosae — endemic New World (primarily North American) clades resolved by molecular data indicate more extensive evolutionary radiations in (especially western) North America than earlier recognized.

Such legume examples include the major radiations of western North American *Lupinus* (tribe Genisteae), with accelerated diversification in the montane perennials (Drummond et al., 2012), and tribe Loteae (including *Acmispon* and *Hosackia*; Allan & Porter, 2000), each with substantial representation in the CA-FP and Californian deserts. North American clades of *Lathyrus* (tribe Fabeae; Schaefer et al. 2012), *Trifolium* (tribe Trifolieae; Ellison et al., 2006), and tribe Psoraleeae (e.g., *Hoita* and *Rupertia*; Egan & Crandall, 2008) also in part represent diversification in the CA-FP, as does the massive radiation of dysploid New World *Astragalus* (tribe Galegeae; Wojciechowski et al., 1999; Scherson et al., 2008; see Rundel et al., 2015).

In the composites, molecular phylogenetic studies have resolved a clade representing the New World taxa of *Cirsium* (tribe Cardueae), including a diverse

CA-FP radiation (Fig. 1d–f; Kelch & Baldwin, 2003), and a clade representing the vast majority of New World taxa in tribe Astereae (Noyes & Rieseberg, 1999; Brouillet et al., 2009), including about a quarter of all Californian species of the sunflower family. Previous taxonomic alignments of North American members of each of those clades with various Old World relatives (e.g., with *Aster*) were evolutionarily and biogeographically misleading, as were taxonomic treatments uniting various Old World members of Filaginae (= the "*Filago* group;" tribe Gnaphalieae) with New World taxa, which constitute a separate clade well represented by California endemics (Galbany-Casals et al., 2010). The primarily North American genera of tribe Cichorieae (e.g., *Malacothrix*, *Microseris*, *Stephanomeria*) also represent an evolutionary radiation with extensive Californian endemic diversity spanning coastal, montane, and desert settings (Lee et al., 2003; Tremetsberger et al., 2013). The clade encompassing most if not all primarily western North American genera of tribe Senecioneae (Pelser et al., 2010) represents modest diversity in number of taxa but extensive disparity in ecology and in vegetative and reproductive morphology, e.g., among *Cacaliopsis*, *Lepidospartum*, *Luina*, and *Tetradymia*.

Phylogenetic data warranting resurrection and expansion of Jepson's tribe Madieae to include the woolly sunflowers (*Eriophyllum* and relatives), goldfields (*Lasthenia*), *Arnica*, and other genera in addition to the tarweed subtribe Madiinae have indicated that multiple California-based radiations belong to a highly diverse, primarily Californian clade (Baldwin et al., 2002). The already extensive chromosome evolution in tarweeds, woolly sunflowers, and goldfields concluded from earlier intensive studies of each group (see Ornduff, 1966; Kyhos et al., 1990; Mooring, 1997) evidently has been even greater based on the apparently high base chromosome number ($x = 19$) for the tribe (Baldwin et al., 2002; Carr, 2003; Semple & Watanabe, 2009), with descending dysploidy to chromosome numbers as low as $2n = 4_{II}$ in tarweeds (in *Calycadenia* and *Holocarpha*) and $2n = 3_{II}$ in woolly sunflowers (in *Pseudobahia*) endemic to California. Relationships resolved in the tribe indicate evolutionarily informative, bidirectional shifts in habit, ecological setting, and chromosome number. In particular, Californian Madieae includes examples of descending dysploidy following ecological transitions from perennial to annual and effectively wetter to drier conditions, and of polyploidy following transitions in the other direction, from annual to perennial and toward more mesic conditions (Baldwin et al., 2002). Those findings are consistent with phylogenomic evidence of paleopolyploidy in Compositae (Barker et al., 2016) and with Stebbins's (1950) chromosomal evolution hypothesis that natural selection favors reduced genetic linkage in self-incompatible annuals of harsh (e.g.,

dry) environments, where only a limited range of trait expressions may be successful.

Additional examples of Californian endemics that arose from more extensive American radiations than previously hypothesized, such as the clade representing the endemic western North American genera of perennial Umbelliferae (Sun & Downie, 2010; George et al., 2014), reinforce the importance of North America in general as the immediate source area for much of the California flora. That interpretation is also consistent with phylogenetic resolution of global-scale floristic disjunctions. Donoghue & Smith (2004) found that most western North American representatives of clades with disjunct taxa spanning Eurasia and North America were more closely related to their eastern North American relatives than to those in Europe or Asia, notwithstanding more recent phylogenetic evidence for additional disjunctions between east Asia and western North America (Wen et al., 2016). Within *Quercus*, for example, phylogenomic analyses indicated that the CA-FP taxa of red oaks (sect. *Lobatae*) and white oaks (sect. *Quercus*) each constitute a clade that is sister to the eastern North American and Mexican taxa of the same section (Hipp et al., 2018, this volume). Even well-supported disjunctions between taxa in the floras of eastern North America and Asia have been suggested to be potentially misleading biogeographically, given the likelihood of higher extinction rates in the floras of western North America (and Europe), where more extreme Cenozoic climatic change may have exterminated the closest relatives of eastern North American disjuncts (Wen et al., 2010).

Phylogenetic investigations of clades spanning different Mediterranean-type climatic areas also have found a paucity of examples of Californian taxa that appear to have originated from relatives adapted to Mediterranean-type climates on other continents. Most historically proposed examples of Mediterranean Basin – Californian disjunctions appear instead to be examples of ecological convergence toward Mediterranean-type conditions in both regions based on clade relationships and ages, although some disjunctions may be best explained by long-distance dispersal from the Mediterranean Basin to California (Kadereit and Baldwin, 2012). Renewed investigations of amphitropical disjunctions between the CA-FP and central Chile have strongly upheld Raven's (1963) conclusion that bird-mediated dispersal from North America to South America since the Pliocene explains the vast majority of such examples (Wen & Ickert-Bond, 2009; Simpson et al., 2017). Most disjunctions between Californian and Australasian flora also appear to be best explained by southward long-distance dispersal (e.g., Vijverberg et al., 1999, 2000; Dierschke et al., 2009).

Phylogenetic evidence for long-distance dispersal from California or western North America more generally to the Hawaiian Islands arguably has led to the greatest change in understanding of the importance of the American Pacific Coast as a biogeographic source for extra-continental areas (see Baldwin & Wagner, 2010). Chloroplast and nuclear DNA data have confirmed and extended Carlquist's (1959) anatomical evidence for a tarweed ancestry of the Hawaiian silversword alliance, with descent of the Hawaiian lineage from the "*Madia*" lineage of California tarweeds ~5.1 Ma (Baldwin & Sanderson, 1998; Landis et al., 2018). Evolutionary radiation of the silversword alliance into trees, shrubs, rosette-plants, mat-plants, cushion-plants, and lianas across dry, wet, and bog habitats of the Hawaiian Islands evidently began only ~3.5 Ma (Landis et al., 2018). Some members of the silversword alliance are ecological dominants, especially at higher elevations, where initial colonization of the islands probably occurred (Baldwin & Wagner, 2010). Molecular phylogenetic data also indicate a far western North American origin of the highly diverse Hawaiian mints (Lindqvist & Albert, 2002; Roy et al., 2015), and the ecologically and morphologically disparate Hawaiian violets (Ballard & Sytsma, 2000: Marcussen et al., 2011) and Hawaiian sanicles (Vargas et al., 1998). These and other examples of American lineages in the Hawaiian flora represent much more diversity and diversification in the islands than most early-to-mid 20th Century botanists and biogeographers believed could be attributable to New World colonists (see Baldwin & Wagner, 2010).

Although most endemic species in California reflect diversification within the timeframe of development of a Mediterranean-type climate in far western North America, disparate lineages of mostly woody CA-FP taxa have been confirmed as paleo-endemics by recent phylogenetic work. Molecular data have corroborated the antiquity of various endemic conifers, such as Santa Lucia fir (*Abies bracteata* (D. Don) Poit., Pinaceae; Xiang et al., 2015) and weeping spruce (*Picea breweriana* S. Watson, Pinaceae; Ran et al., 2015), and the near-endemic incense cedar (*Calocedrus decurrens* (Torr.) Florin, Cupressaceae; Chen et al., 2009), as well as xeric-adapted or preadapted woody endemic eudicots, such as *Aesculus californica* (Spach) Nutt. (Sapindaceae; Harris et al., 2009), *Carpenteria californica* Torr. (Hydrangeaceae; Guo et al., 2013), *Cneoridium dumosum* (Nutt. ex Torr. & A. Gray) Hook.f. ex Baill. (Rutaceae; Salvo et al., 2010), *Malosma laurina* (Nutt.) Nutt. ex Abrams (Anacardiaceae; Yi et al., 2004), and *Pickeringia montana* Nutt. (Leguminosae; Wojciechowski, 2013). For the California Islands, where paleo-endemism has been well established for the Channel Islands genus *Lyonothamnus* (Rosaceae; Raven & Axelrod, 1978; Erwin & Schorn, 2000), recent phylogenomic work determined that the only CA-FP vascular plant genus to go extinct in historical time, *Hesperelaea* (Oleaceae), also represents a paleo-endemic,

known only from Guadalupe Island (Zedane et al., 2015). DNA sequences from the first and only known collection of the sole species, *H. palmeri* A. Gray, by Edward Palmer in 1875, were successfully obtained by genome skimming and included in phylogenetic analyses of subtribe Oleinae. Those results demonstrated that the *Hesperelaea* lineage diverged from a common ancestor with its closest living relatives (*Forestiera* and *Priogymnanthus*) during early-to-mid Miocene, prior to emergence of Guadalupe Island. Removal of feral goats from Guadalupe Island more than a dozen years ago has resulted in extensive revegetation of the once denuded landscape and rediscovery of presumed-extinct endemic plants there (Garcillán et al., 2008), but not *Hesperelaea*, which we now understand to be an even more tragic loss of phylodiversity than earlier appreciated.

Spatial patterns of Californian plant diversity and endemism from phylogenetic and species-based perspectives. The NSF-funded California Plant Phylodiversity Project (CPPP) at the University and Jepson Herbaria [principal investigator (PI), B.D. Mishler; co-PIs, D.D. Ackerly and B.G. Baldwin] recently revisited spatial patterns of vascular plant diversity and endemism across the state, using specimen-based, taxonomically comprehensive approaches, with and without incorporation of molecular phylogenetic data (Baldwin et al., 2017; Thornhill et al., 2017; Kling et al., 2018). Earlier studies of patterns of species richness and endemism in California led to fundamental advances, such as delimitation of the CA-FP endemism hotspot (Howell, 1957), explicit recognition of paleo-endemic and neo-endemic components of the California flora (Stebbins & Major, 1965), and the importance of mesic- and xeric-preadapted lineages in California's floristic assembly (Raven & Axelrod, 1978). The CPPP was able to examine relatively fine-scale spatial patterns of diversity and endemism using (1) a comprehensive set of equal-sized spatial units (15 × 15 km grid cells), (2) raw coordinate-based and climate-modeled geographic range estimates for each species or clade, and (3) a maximum-likelihood phylogenetic tree spanning the entire Californian vascular flora (Baldwin et al., 2017; Thornhill et al., 2017). Those advances were made possible by recent growth of herbaria databases with georeferenced specimens such as the Consortium of California Herbaria (http://ucjeps.berkeley.edu/consortium/; see Markos et al., 2016), development of a taxonomically updated vascular flora of California — the *Jepson eFlora* (Jepson Flora Project, 2016), and availability (in GenBank) and generation of chloroplast and nuclear DNA sequences for a set of 1083 terminal clades (operational taxonomic units, OTUs) to which nearly every Californian species could be reliably assigned (Thornhill et al., 2017). Recently developed metrics and analyses for species-based and phylogenetic studies of spatial patterns of richness and

endemism (see below) also allowed for new floristic insights, including the areas of highest conservation priority for protecting Californian plant diversity.

Patterns of species richness (= number of species in an area, e.g., in a spatial grid cell) and phylodiversity (= sum of phylogenetic branch lengths for all lineages in an area; Faith, 1992) across California (Baldwin et al., 2017; Thornhill et al., 2017) reinforced earlier findings (Stebbins & Major, 1965; Qi & Yang, 1999; Thorne et al., 2009) on the floristic importance of the CA-FP in general and of areas of high topographic and climatic heterogeneity, especially in the coastal and montane CA-FP. Additional analyses involved derived metrics, such as weighted endemism (Crisp et al., 2001), which inversely weighs species by their range size, thereby giving greater weight in an individual grid cell to species that are found in fewer grid cells across California; the comparable phylogenetic metric, called phylogenetic endemism (Rosauer et al., 2009), inversely weighs phylogeny branches by their range size, thereby giving greater length to branches found in fewer grid cells. In other words, weighted endemism is to species richness as phylogenetic endemism is to phylodiversity, and both metrics reflect relative endemism (sensu Thornhill et al., 2018) or range-weighted diversity, as opposed to unqualified, absolute endemism, which dictates that taxa (or branches) must be completely restricted to a particular area or setting to be considered endemic there. Areas of high weighted endemism and phylogenetic endemism in the CA-FP were comparable to those of high species richness and high phylodiversity but less extensive overall, generally in higher montane and outer coastal areas, where concentrations of range-limited taxa or lineages are evident (Baldwin et al., 2017; Thornhill et al., 2017).

The CPPP also brought into focus the floristic importance of Californian regions of drier climate — including the deserts, outside the CA-FP. For the species-based (non-phylogenetic) analyses (Baldwin et al., 2017), areas of high corrected weighted endemism (= weighted endemism / species richness; Crisp et al., 2001), i.e., a metric that corrects weighted endemism for species richness, were concentrated largely at higher elevations of the Great Basin and Mojave deserts, as well as the Klamath Ranges (northwestern California) and Channel Islands (southwestern California). These same areas were among those found to harbor significantly high relative endemism, i.e., in the top 5% of the distribution of random values from a spatial randomization (999 replicates) that kept constant the number of species per grid cell and number of cells occupied per species (Baldwin et al., 2017). The higher ranges of the southern Great Basin and Mojave deserts (as well as the Channel Islands and the higher Klamath Ranges) were found to remain high in corrected weighted endemism and significantly high in endemism in

analyses including only species that are absolute endemics of California — in other words, for those areas the findings were not an artifact of restricting the analyses to California to the exclusion of extensive desert lands outside the state (Baldwin et al., 2017).

The phylodiversity and phyloendemism findings brought an additional, evolutionary context to the spatial diversity patterns, with general implications for understanding the ecological and regional history of assembly of the California flora, including the desert flora. For example, results from spatial randomization tests of phylogenetic diversity and of "relative phylogenetic diversity" (= comparison of actual phylogenetic diversity with phylogenetic diversity for the same tree topology but with all branches of equal length; Mishler et al., 2014) indicated that the California deserts and substantial portions of the drier southern half of the CA-FP — especially the San Joaquin Valley, South Coast Ranges, and Transverse Ranges — have significantly low phylodiversity, with a significantly high concentration of short phylogeny branches (Thornhill et al., 2017). Areas of significantly high phyloendemism also tended to be concentrated toward the dry end of the precipitation spectrum, with the main concentration of areas of significantly high neo-endemism located outside the CA-FP in mountains of the Inyo region, such as the White-Inyo Range, and the eastern Mojave Desert (Thornhill et al., 2017). These findings build on results of an earlier, less exhaustive spatial diversity study of Californian neo-endemism by Kraft et al. (2010), who found the flora of the southern California deserts and dry regions flanking the San Joaquin Valley to be especially young, in line with the youth of desert or desert-like conditions in those areas. More generally, as pointed out by Thornhill et al. (2017), these results conform to Stebbins's (1952) hypothesis of aridity as an evolutionary stimulus. The evolutionary importance of island-like conditions may also be reflected by the concentration of neo-endemism in the "sky island" desert mountains, as well as the oceanic Channel Islands, which also were low in species richness and phylodiversity but significantly high in species-based relative endemism and phyloendemism (Thornhill et al., 2017).

Phyloendemism also has been incorporated recently in prioritization of California lands for protection of floristic diversity. As primary conservation goals, the CPPP gave priority to areas containing a high diversity of long-branch lineages (i.e., high phylodiversity) that are poorly protected throughout narrow geographic distributions, i.e., that occur in a small number of poorly protected grid cells (Kling et al., 2018). Given the great extent of both habitat destruction and various degrees of land protection across much of California, the analyses incorporated spatial data on current habitat integrity and land protection status across the state to ensure that

low conservation priority be given to now-degraded areas of historically high phylodiversity as well as areas already well protected. Our reliance on herbarium specimens spanning >100 years of collecting to inform Californian plant distributions necessitated consideration of current habitat intactness in those calculations.

Ranking all grid cells across California for conservation priority based on phyloendemism versus (non-phylogenetic) weighted endemism yielded non-identical but overlapping results (Kling et al., 2018). The top-50 conservation priorities based on phyloendemism, weighted endemism of species, or weighted endemism of operational taxonomic units (OTUs, representing one or more species) of the phylogenetic analyses were all in the CA-FP, and each included common areas of the northern Sierra Nevada foothills, northern South Coast Ranges (i.e., Mt. Hamilton Range), and portions of the northern and southern Inner and Outer Coast Ranges and outer coast. High conservation priorities in the full analyses included some areas of significantly high species-based endemism or phyloendemism, such as parts of the San Francisco Peninsula, some of Stebbins and Major's (1965) endemic areas of the central Coast Ranges (e.g., "Hamilton" — noted above, "Monterey," and "Santa Cruz"), and San Clemente and Santa Catalina islands (southern Channel Islands).

Extensive differences between the quilt of areas identified in the phyloendemism analyses as high conservation priorities and those identified as priorities in a "blank-slate" analysis that did not consider land protection status or habitat intactness demonstrated the floristic importance of currently protected areas and those that have been lost or compromised by human-related impacts (Kling et al., 2018). In general, areas of high conservation priority in the full analyses were more concentrated in near-coastal and foothill areas of the CA-FP (Fig. 1g) than in the blank-slate analyses, which more highly prioritized upper montane areas of the CA-FP and deserts that are mostly already protected to some degree (Fig. 1h). Areas of significantly high species-based endemism or phyloendemism that were high conservation priorities in the blank-slate analyses but not the full analyses included the high Klamath Ranges, Mount Shasta vicinity, upper elevations of the central and southern Sierra Nevada, and the high San Bernardino Mountains (Transverse Ranges) of the CA-FP; the Sweetwater Mountains and White-Inyo Range of the Great Basin; and the high ranges of the eastern Mojave Desert (e.g., Clark Mountain Range and New York and Providence mountains). On a finer spatial scale, reduced conservation priority of some areas, such as much of the Los Angeles Basin, the San Diego vicinity, and parts of the San Francisco Bay Area, in

the full analyses compared to the blank-slate analyses reflects extensive habitat loss or degradation by human activities.

Conclusions. Estimates of CA-FP diversity and diversification continue to rise with increasing attention to resolving fine- and broad-scale phylogenetic relationships in the California flora, and underscore the CA-FP as a global-scale biodiversity hotspot (Mittermeier et al., 2011). From an evolutionary perspective, the relative importance of factors that likely have contributed to high richness and endemism in the CA-FP is still uncertain, although most CA-FP lineages with endemic diversity post-date the mid-Miocene shift toward summer-drying that ultimately led to the Mediterranean-type climate characteristic of the area (see Baldwin, 2014). On a spatial scale, high floristic richness in California is strongly associated with areas of high topographic and substrate heterogeneity, where close proximity of diverse climatic and habitat conditions may have promoted high speciation or low extinction rates (Raven & Axelrod, 1978; Lancaster & Kay, 2013; Baldwin, 2014; Baldwin et al., 2017; Thornhill et al., 2017). Significantly high endemism — higher than expected based on levels of floristic richness — and concentrations of young lineages are especially notable in drier regions of California, including the southern Great Basin and warm deserts, where "sky islands" show high concentrations of neo-endemism, as do California's oceanic Channel Islands (Thornhill et al., 2017). California's current network of protected lands is important for conserving the high richness and endemism associated with upper montane areas of the CA-FP and deserts (Kling et al., 2018), where floristic vulnerability to anthropogenic climate change may be buffered to some extent by environmental heterogeneity (Ackerly et al., 2010) but needs more study. Under-protected lands of highest priority for floristic conservation largely occur in the CA-FP coastal and foothill regions (Kling et al., 2018), where ever increasing development pressure and escalating land prices warrant quick action to safeguard the most floristically precious areas (see Riordan & Rundel, 2014; Moanga et al., 2018; Syphard et al., 2018).

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Figure 1. —A–C. Representatives of evolutionarily distinct lineages of the *Collinsia* "metamorphica" complex (Plantaginaceae), central Sierra Nevada, California. Photos by Michael S. Park. —D–F. Representatives of the endemic California Floristic Province clade of *Cirsium* (Compositae). D. *C. douglasii* DC. var. *breweri* (A. Gray) D.J. Keil & C.E. Turner, from wet sites. Photo by Neal Kramer. E. *C. fontinale* (Greene) Jeps. var. *fontinale*, from serpentine seeps. Photo by Toni Corelli. F. *C. rhothophilum* S.F. Blake, from coastal dunes. Photo by Chris Winchell. —G–H. Conservation prioritization of Californian lands based on floristic phyloendemism under three representations of the molecular phylogenetic tree for California vascular plants: a chronogram with branches scaled to time using fossil calibration (valuing survival time or duration of lineages, in pink), a

cladogram with all branch lengths equal (valuing diversification, in yellow), and a phylogram with branches reflecting inferred mutational change (valuing genetic divergence, in pale blue). Darkness of colors indicates higher priority (light areas are lower priority); deep blue, red, and green indicate priority under two schemes and black indicates priority under all three schemes (see Venn diagram). Modified from Kling et al. (2018). G. Results of the full analysis, down-weighting areas already protected and areas of reduced habitat integrity. H. Results of "blank-slate" analysis, not considering current land protections or habitat integrity.